

The West Palaearctic *Dineura* species, focussing on Sweden (Hymenoptera, Tenthredinidae)

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Abstract

Four *Dineura* species are now considered to occur in the West Palaearctic, including northern Europe, but *D. parcivalvis* has not been found in Scandinavia. *Dineura pullior* Schmidt & Walter, 1995 is treated as a new junior subjective synonym of *D. virididorsata* (Retzius, 1783). An illustrated key to adults is presented. Lectotypes are designated for seven nominal taxa: *Dineura stilata* var. *virilis* Enslin, 1918, *Dineura testaceipes* var. *nigriventris* Enslin, 1915, *Dineura virididorsata* var. *dorsalis* Enslin, 1915, *Nematus posticus* Förster, 1854, *Nematus xanthocerus* Hartig, 1840, *Nematus xanthopus* Zaddach, 1876, and *Tenthredo (Allantus) stilata* Klug, 1816. Distributions in the Fennoscandian countries are outlined, with particular reference to Sweden.

Key words: Symphyta, Nematinae, sawflies, key, taxonomy, distribution

Introduction

The sawfly genus *Dineura* Dahlbom, 1835 has recently been considered to contain ten described extant species, eight of which have been found in the Palaearctic Realm (Taeger *et al.* 2010, Hara & Shinohara 2018), with *D. militaris* (Cresson, 1880) as the single Nearctic representative (Prous *et al.* 2014), and *D. sharkeyi* Smith, 2011 only known in Thailand (Smith 2011). Five species have recently been treated as occurring in Europe (Taeger *et al.* 2006) and the West Palaearctic (Lacourt 1999). Adults can be recognised as belonging to the genus using the key to Nematinae genera by Prous *et al.* (2014). Our main objective here is to present an illustrated key to the West Palaearctic species, and outline their distribution in Fennoscandia, with particular reference to Sweden.

Material and methods

The names of collections referred to in the text are abbreviated as follows:

BMNH	The Natural History Museum, London, United Kingdom
FMNH	Finnish Museum of Natural History, Helsinki, Finland
MSNG	Museo Civico di Storia Naturale “Giacomo Doria”, Genova, Italy
MZLU	Lunds universitet, Entomology Collection, Lund, Sweden
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
ZMHUB	Naturkundemuseum, Berlin, Germany
ZSM	Zoologische Staatssammlung, Munich, Germany

Registration numbers of specimens allocated by the SDEI (five digits, omitting the prefix „DEI-GISHym“) are cited in the figure captions, thus enabling the corresponding collection data to be located in the text. Morphological terminology follows Viitasaari (2002), except for the use of sawtooth instead of serrula (see Malagón-Aldana *et al.* 2017).

Genitalia were macerated in 10–15% KOH at room-temperature for four to five hours before being mounted temporarily in glycerine on glass slides for photography. Alternatively, they were cleared in proteinase during DNA extraction. After photography, the dissected parts were gummed with Berlese fluid to a card fixed to the specimen’s pin.

To estimate phylogenetic relationships between *Dineura* species, we used sequences of four gene fragments, one mitochondrial (COI) and three nuclear (NaK, POL2, TPI), which were sequenced as described by Prous *et al.* (submitted). For mitochondrial COI barcode data, minimal p-distances (proportion of differences) between and maximal distances within BIN (Barcode Index Number) clusters were taken from BOLD (<http://www.boldsystems.org/>) BIN database. Some of the COI barcode sequences used here were obtained from BOLD (<http://www.boldsystems.org/>). In this case, DNA extraction, PCR amplification, and sequencing were conducted at the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Canada, using standardised high-throughput protocols (Ivanova *et al.* 2006, deWaard *et al.* 2008), available online under www.ccdb.ca/resources.php. DNA aliquots of SDEI vouchers are deposited in the DNA storage facility of the SDEI (including those that were originally extracted at the CCDB).

Results

Character assessment

Genetic data. During the past few years, genetic data (mainly COI barcodes) for all the European *Dineura* species have become available (Fig. 1). In BOLD Systems, specimens of *stilata* are distributed between two BINs (Barcode Index Number Uniform Resource Identifier, in BOLD Systems: boldsystems.org), one of which is shared with *testaceipes*. *Dineura virididorsata* and *pullior* specimens share a single BIN (see Schmidt *et al.* 2017). Apparently only the barcode of *parcivalvis* is sufficiently distinctive to permit unequivocal determination using this method. Because nuclear data gives similar results to COI barcodes we combined all genes in a single dataset by including the specimens for which at least COI and one nuclear gene (TPI) were available (Fig. 1). *Dineura virididorsata* and its form previously known as *pullior* (males identified based on head colouration) are genetically very close and cannot be separated from each other, but are rather distant from other *Dineura* species (Fig. 1). Genetic distance between *virididorsata* and *pullior* (based on one mitochondrial and two nuclear genes, 0.2–0.3%) is well within the range of intraspecific variation, judging from the number of heterozygous sites (see Fig. 1) observed for females in nuclear genes of other *Dineura* species (0.0–0.5%). *Dineura parcivalvis* separates well from other species also based on nuclear genes (Fig. 1). Although the sampling is limited, *stilata* and *testaceipes* seem to separate from each other (1.2% based on combined COI and TPI) (Fig. 1). There seem to be two additional species (Fig. 1) in the East Palaearctic (specimens sampled in Primorsky Krai, Russia) that are morphologically most similar to *parcivalvis*. Judging from the original description, one of the two could be *D. blanki* Wei, 2002 described from China (Henan), although the clypeus of the Russian specimens seems to be more deeply emarginated (1/2 or more of its length) compared to *blanki* (1/3 of its length). Because the two possible species from Primorsky Krai (Fig. 1) are morphologically highly similar, it is difficult to decide without additional studies which of them could be *D. blanki*.

Genitalia. Lindqvist (1955) pointed out that *Dineura testaceipes* and *parcivalvis* have differently shaped penis valves, and Schmidt & Walter (1995) included male and female genitalia characters in their comparison of *pullior* with *virididorsata*. Otherwise, little use has been made of genitalia characters in previous treatments of *Dineura*. Schmidt & Walter (1995) discussed the problem of the altered appearance of lancets of *pullior* and *virididorsata*, particularly the sawteeth, caused by wear. However, we strongly suspect that the wide range of shapes of the saw-teeth observed by us in *virididorsata* is underlain by natural variability existing even before the sawteeth become abraded. Schmidt & Walter concluded that other lancet characters, such as setation of the lamnium and morphology of the radix, are nevertheless still of use for identification of *pullior* and *virididorsata*. Finally, our studies led us to a different conclusion. Because of problems defining species limits using external characters (e.g. colour, see below), and probable overlap in the range of variability of similar species, we strongly recommend examination of genitalia during identification of males.

Colour. Because very few other reliable external characters for distinguishing *Dineura* adults have been found, much importance has been attached to differences in colour pattern. The colour of the head capsule, used in several previous keys, is a very obvious and apparently reliable character for separating *virididorsata* from the other three West Palaearctic species. Although Enslin (1915) wrote that *stilata* rarely has small yellow flecks on the orbits, we have not seen such specimens, even among those with extremely pale body coloration. Two males with pale-marked orbits standing under the names *stilata* and *testaceipes* in the SDEI collection proved to be misidentified *Euura* specimens. Differences in body colour pattern have also previously been the main method of separating *stilata* from *testaceipes*. Although there is a clear trend in these species towards darker abdominal terga in *testaceipes*, specimens might be found which fall in an overlapping range of variability. While colour characters provide an initial indication of the probable identity of a specimen, it is frequently impossible to achieve a reliable identification using colour alone.

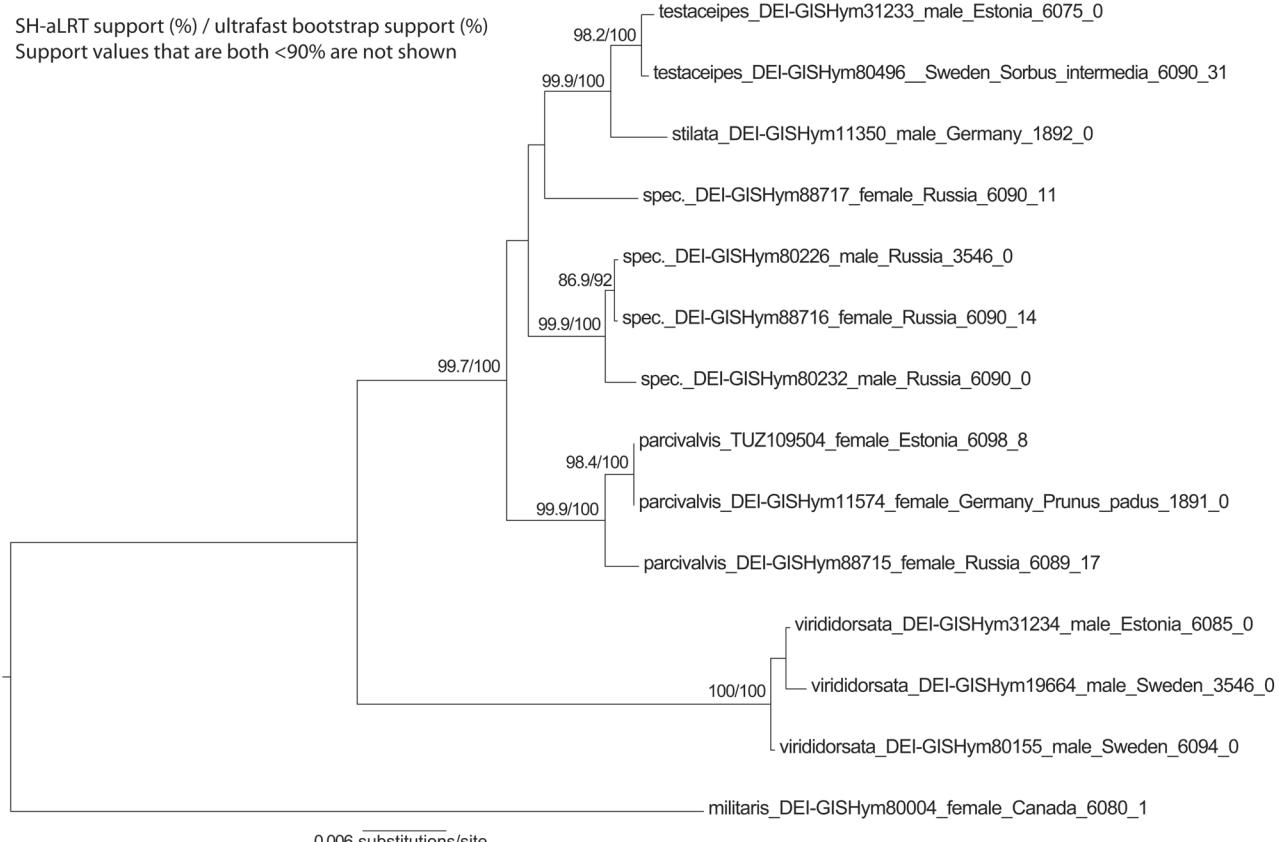


FIGURE 1 Maximum likelihood tree of *Dineura* based on four genes (COI, NaK, POL2, TPI). Included in the analyses were specimens sequenced at least for COI and one nuclear gene (TPI). Best-fit model chosen according to Bayesian information criterion was TIM2+R2. Numbers above branches show SH-aLRT support (%) / ultrafast bootstrap support (%) values. Support values for weakly supported branches (<90) are not shown. Numbers at the end of the tip labels refer to the length of the sequence and the number of ambiguous positions (e.g. heterozygosities). *Dineura militaris* was used to root the tree. Specimen DEI-GISHym19664 was previously determined as *D. pullior*. The scale bar shows the number of estimated substitutions per nucleotide position.

Venation. In all European *Dineura* species, forewing vein 2r-rs may be fully developed, incompletely developed, or completely absent. Lindqvist (1955, 1972) thought that 2r-rs is always absent in *parcivalvis*, but the character state is also variable in this species, e.g. absent in the lectotype, and present in the two females from Brandenburg. Unlike the variable presence / absence of forewing vein 2r-m in gall-making *Euura* species, where the vein is frequently absent in one wing but present in the other of the same individual (Liston *et al.* 2017), the degree of development of 2r-rs in *Dineura* is symmetrical.

Larvae. [slightly modified from Lorenz & Kraus (1957) and Macek 2015] General appearance (Fig. 2). Head spherical, densely covered with erect long setae; vertex (including parietal areas and occiput between lateral sutures) with network of granular texture; diameter of ocularium shorter than malar space; antennae flat, not conspicuous; clypeus with four setae; labrum symmetrical, slightly emarginate anteriorly, with four setae; mandibles with one

seta on the outside edge; maxillae with one seta on stipes, palpifer with two to three setae. Abdomen from thorax tapering posteriorly with flattened ventral side; thorax widened and convex with enlarged lateral lobes of meso- and metathorax; abdomen with prominent subspiracular and surpedal lobes; cuticle with fine granular texture; abdominal segment 3 with six annulets [not five as stated by Lorenz & Kraus (1957) in the text, although figured correctly], with setae on annulets 1, 2 and 4, mostly on more or less prominent warts; anal segment with long setae, inner side of prolegs with two to three short setae.

The larvae of *stilata*, *testaceipes* and *virididorsata* were described by Macek (2015), and according to him are clearly distinguished from each other by the shape and distribution of setae on the abdomen. The larva of *parcivalvis* has not been described. In general appearance, and because of its short setae and inconspicuous glandulae, the larva of *virididorsata* strongly resembles that of *Nematinus acuminatus* (Thomson, 1871), which also feeds on *Betula*, but abdominal segment 3 of the latter has only five annulets, of which 1, 2, 3 and 4 bear setae.

Life history: general

Oviposition is usually in the leaf-petiole, sometimes in the base of a main vein in the leaf blade, at least in *virididorsata* (Walter *et al.* 1994). The larvae skeletonise the upper surfaces of leaves, but usually rest in a stretched attitude on the undersides of the leaves (Macek 2015). They develop very slowly, so that the feeding period can last for more than three months (Pschorr-Walcher & Altenhofer 2000). Eonymphs burrow into the upper soil layers, rotten wood, or even fungi and birds' nests, where they spin a firm cocoon in which the praepupa hibernates (Macek 2015; unpublished observations by AL). All species are univoltine, with emergence in the year following larval development (Pschorr-Walcher & Altenhofer 2000).

Key to West Palaearctic *Dineura* species (imagines)

Notes: The distinction of *stilata* and *testaceipes* using the colour characters presented here should be unproblematic for specimens from more northern parts of Europe, including Fennoscandia, where no overlap in colour pattern of these taxa has been observed. In more southerly regions of Europe, some specimens of *testaceipes* are extremely pale, and probably not always distinguishable from *stilata* (compare, for example, figs 1 and 2 in Macek 2015).

- | | | | |
|------|----|--|--|
| 1 | a | Head with at least orbits and temples extensively pale (Figs 3–6) | |
| | b | Mesepisternum mainly pale; at most narrowly blackish on dorsal and ventral margins (Fig. 11) | |
| | c | Antenna entirely pale (Figs 8–11) | <i>Dineura virididorsata</i> (Retzius, 1783) |
| - | aa | Upper head completely black (Fig. 7); pale are at most mouthparts and supraclypeal area | |
| | bb | At least lower half of mesepisternum <i>usually</i> black (Figs 13, 18–19) | |
| | cc | Antenna <i>usually</i> black-marked, at least on scape (Figs 7, 12–18) | 2 |
| 2(1) | a | ♀♀ | 3 |
| - | aa | ♂♂ | 5 |
| 3(2) | a | Dorsum of abdomen predominantly pale (only tergum 1, 2 and sometimes partly 3 dark) (Fig. 12); venter always pale (Fig. 13) | |
| | b | <i>Only applicable to Fennoscandian specimens</i> : upper mesepisternum pale (Fig. 13) | <i>Dineura stilata</i> (Klug, 1816) ♀ |
| - | aa | Dorsum of abdomen <i>usually</i> predominantly black (or at least some terga other than 1 and 2 medially dark) (Figs 15–16); venter pale or dark | |
| | bb | <i>Only applicable to Fennoscandian specimens</i> : whole mesepisternum dark (as Fig. 18) | 4 |
| 4(3) | a | Antennomeres 8 and 9 in narrowest view at most 4.5 × as long as greatest width (Fig. 19) | |
| | | | <i>Dineura testaceipes</i> (Klug, 1816) ♀ |
| - | aa | Antennomeres 8 and 9 in narrowest view at least 5.0 × as long as greatest width (Fig. 20) | |
| | | | <i>Dineura parcivalvis</i> (Konow, 1901) ♀ |
| 5(2) | a | At least middle abdominal terga extensively pale (Fig. 14); abdominal sterna always pale . . . | <i>Dineura stilata</i> (Klug, 1816) ♂ |
| - | aa | All abdominal terga mainly dark (Fig. 18); abdominal sterna pale or dark. | 6 |
| 6(5) | a | Penis valve paravalva distally with ventral valvispina longer and basally narrower than dorsal valvispina (Figs 32–33) | |
| | b | Antennomere 8 less than 4 × as long as broad (Fig. 21) | <i>Dineura testaceipes</i> (Klug, 1816) ♂ |
| - | aa | Penis valve paravalva distally with ventral and dorsal valvispina nearly equal in length and basal width (Figs 34–35) | |
| | bb | Antennomere 8 more than 4 × as long as broad (Fig. 22) | <i>Dineura parcivalvis</i> (Konow, 1901) ♂ |

Species treatments

Dineura parcivalvis (Konow, 1901)

Pontania parcivalvis Konow, 1901a: 83 [key], subsequent description Konow 1901b: 128. Syntypes ♀, **lectotype** ♀ (DEI-GISHym31791, images: <https://doi.org/10.6084/m9.figshare.7851215>), designated by Lindqvist (1955) by inference of “holotype”, examined, in SDEI. Type locality: Livonia, Dorpat [= Estonia, Tartu].

Dineura parcivalvis: Conde (1938); new combination, treated as synonym of *Dineura stilata* var. *testaceipes*.

Taxonomy. Treated here as separate from *testaceipes* because of its different genetics (Fig. 1), larval host, and penis valve morphology.

Additional description. Body length: ♀ 4.5–6.0mm, ♂ 4.5–5.0mm. Female (Fig. 17): Head black, except for brown labrum, and sometimes anterior of clypeus and underside of antennal flagellum. Thorax black, except for pale tegula, more or less pronotum, and legs. Sterna of abdomen and downturned lateral parts of terga from largely pale to nearly completely black; dorsum of abdomen black. Pterostigma uniformly brown. The five examined European female *parcivalvis* are very similar in colour at least to two specimens examined from Primorsky Krai, with the pronotum and venter of the abdomen extensively pale. However, we cannot exclude the possibility that there are darker specimens with darker venter and pronotum, which could be confused with possible additional species in East Palaearctic (Fig. 1). Lancet: Fig. 27. Male (Fig. 18): Coloration and variability similar to female: the single examined European male very pale. Penis valve: ventral spine about as long as dorsal one; ventral spine rather abruptly tapering after medial constriction, and distal portion about as long as basal portion (Figs 34–35).

Total number of specimens examined: 1♂, 7♀.

Similar species. Morphology and coloration very similar to *Dineura testaceipes*. Liston (2015) presented some characters, several of which had already been proposed by Lindqvist (1955), that were thought to be suitable for separating the females of *parcivalvis* and *testaceipes*. After checking a larger number of specimens of both species (identified primarily by barcoding, or because they were reared from *Sorbus*), all these characters were found to be so variable in both species, except apparently for the proportions of the distal antennomeres, that they can no longer be recommended for determination. The males are distinguishable by differences in their penis valves (see key), but the female lancets are very similar, particularly the lamnium. Perhaps the shape of the tangium may be diagnostic, but this needs to be checked for a larger number of specimens: in *parcivalvis* tangium roughly triangular and higher in proportion to length (Fig. 27) than the proportionately lower and more rhomboid tangium of *testaceipes* (Fig. 26).

Life history. Host plant: *Prunus padus* (Kontuniemi 1960).

Distribution. Estonia (Taeger *et al.* 2006; the record from Latvia is probably in error for Estonia, according to Viitasaari *et al.* 1998), Finland, Belarus (Pankevich 1973), ?Czech Republic (Lindqvist 1955), Germany, and Russian Far East (Liston 2015). Occurrence in Sweden: published records: none. Material examined: none.

Specimens examined. Finland: 1♂, Helsinki, leg. O. Winter (<http://id.luomus.fi/GL.2412>) (FMNH). Germany: 2♀, Brandenburg, Waldsieversdorf, 19.05.2006 (DEI-GISHym11575), 25.05.2006 (DEI-GISHym11574), leg. Liston (SDEI). Russian Far East: 2♀ (including DEI-GISHym88715).

Dineura stilata (Klug, 1816)

Tenthredo (Allantus) stilata Klug, 1816: 82–83. Syntypes ♀, “in hiesiger Gegend” [= Berlin area]; **lectotype** ♀ here designated, in ZMHUB (GBIF-GISHym2756, images: <https://doi.org/10.6084/m9.figshare.7851272>).

Type locality: Berlin (Germany). Paralectotypes: 2 ♀ (GBIF-GISHym2757 and 2758), same data as the lectotype, in ZMHUB. *Nematus apicalis* Stephens, 1835: 32. Syntypes, sex not stated, Coomb Wood near London, possibly in BMNH, not examined.

Synonymy with *stilata* by Cameron (1885).

Selandria scapularis Stephens, 1835: 46. Syntypes, sex not stated, near London, possibly in BMNH, not examined. Synonymy with *stilata* by Konow (1905).

Nematus xanthocerus Hartig, 1840: 23. Syntypes, sex not stated, “Nordeutschland” [according to introductory text]; **lectotype** ♀ here designated, in ZSM (GBIF-GISHym3099, images: <https://doi.org/10.6084/m9.figshare.7851299>). Type locality: northern Germany. Paralectotypes: 1♀ (GBIF-GISHym3098), 1♂ (GBIF-GISHym3100), same data as the lectotype, in ZSM. Synonymy with *stilata* by Dalla Torre (1894).

Nematus posticus Förster, 1854: 349–350. Syntypes ♂, near Aachen; **lectotype** ♂ here designated, in ZSM (GBIF-GISHym3091,

- images: <https://doi.org/10.6084/m9.figshare.7851314>). Type locality: Aachen. Paralectotypes: 5♂ (GBIF-GISHym3092 to 3096), same data as the lectotype, but undated, in ZSM. Synonymy with *Nematus xanthocerus* by Wüstnei (1885).
- Nematus xanthopus* Zaddach, 1876: Plate III, Fig. 5. Syntypes larvae [subsequent description of adult by Brischke (1883): 167–168]; Danzig, Schottland, Elberfeld, München, Hamburg, Halle, Kopenhagen, Harz; **lectotype** ♀ here designated, in ZMHUB (GBIF-GISHym2760, images: <https://doi.org/10.6084/m9.figshare.7851338>). Type locality: Copenhagen. Synonymy with *Nematus xanthocerus* by Wüstnei (1885).
- Dineura melanoxantha* Zaddach, in Brischke, 1883: 232–233. Syntypes ♀♂, Rostock, material lost. Listed in synonymy with *stilata* by Blank & Taeger (1998).
- Dineura sulcifrons* Konow, 1885: 296–297. Syntypes ♀♂, “Corvin an der Persante” [now in Poland: West Pommerania, Powiats Bialogardzki and Świdwiński], type material lost. Synonymy with *stilata* by Konow (1905).
- Dineura sulcata*: Konow (1890), misspelling of *sulcifrons*.
- Dineura nigro-flava* Magretti, 1886: 24–25. Holotype ♂ (SDEI-GISHym956, images: <https://doi.org/10.6084/m9.figshare.7856762>), Senago (Italy), in MSNG. Synonymy with *stilata* by Konow (1905).
- Dineura stilata* var. *virilis* Enslin, 1918: 732. Syntypes ♀, type locality not stated; **lectotype** ♀ here designated, in ZSM (GBIF-GISHym3097, images: <https://doi.org/10.6084/m9.figshare.7851413>). Type locality: Denmark.
- Nematus v-flavum* Cameron, 1882: 537. Syntypes ♀, type locality not stated, possibly in BMNH, not examined. Tentative synonymy with *stilata* by Morice (1906).

Taxonomy. Enslin (1915) treated *stilata* and *testaceipes* as separate species, which he distinguished using colour characters. The range of variability which he described for each taxon fits quite closely with our observations. Since then there has been some controversy about the status of *stilata* and *testaceipes*. Conde (1938) may have been the first specialist to treat them as conspecific, but he did not explain why he did so. Lindqvist (1955) examined the genitalia of specimens which he held to represent *stilata* and *testaceipes*, and found no significant differences. He concluded from this observation, and because he thought that the larvae are “sehr gleichartig” [very similar], that “*testaceipes* kaum für eine eigene, jedenfalls keine gute Art, sondern nur für eine Farbenform von *stilata* gehalten werden kann” [*testaceipes* can hardly be held to be a distinct, and in any case not for a good species, but only as a colour form of *stilata*]. However, it later transpired that what he identified as *stilata* were pale individuals of *testaceipes*: *Dineura stilata* is not at present known in Finland. Benson (1958) treated them as separate species, separated only by the colour pattern of the abdomen. Pschorr-Walcher & Altenhofer (2006) discussed the taxonomic problem in the light of observations on larvae: [translated from German] “*Dineura testaceipes* (Klug) [...] Larvae collected end IX/03 from rowan (*Sorbus aucuparia*) near Schrems in the Waldviertel. Imagines emerged in the following year from end V to start VI. The species is said (as for *D. stilata* (Klug)) to occur also on hawthorn (*Crataegus*) (Taeger et al. 1998). The separation of the two species using variable colour characters seems unreliable, particularly as the saws and male genitalia can hardly be distinguished (Lindqvist 1955). Foodplant-choice tests with *D. stilata* (Martens 1989) indicate rather the existence of hostplant races (*D. testaceipes* on *Sorbus*, *D. stilata* on *Crataegus*) or the effects of conditioning (preference for the host plant on which the larvae developed). Further rearing would be desirable”. The study by Macek (2015) presents a rather different conclusion: *stilata* and *testaceipes* are separate species, clearly distinguished by larval morphology, with *testaceipes* using both *Sorbus* and *Crataegus* as hosts, but *stilata* only on *Crataegus*. Here, we follow Macek’s (2015) opinion, which is supported by small but constant differences between the penis valves of *stilata* and *testaceipes*. Nevertheless, the taxonomy of these taxa would benefit from further study, preferably including additional sequence data for nuclear genes.

Additional description. Body length: ♀ 5.0–6.3 mm, ♂ 4.9–5.7. Head black, labrum and clypeus more or less pale. Scape and pedicel black (Fig. 7); flagellum dorsally dark and ventrally pale, or completely pale in some males. Pterostigma pale, with margins more or less darkened. Female (Figs 12–13): meso- and metanotum completely black, or mesoscutal lobes more or less pale-bordered. Upper mesepisternum extensively pale. Abdomen completely pale, apart from mostly black tergum 1, and sometimes smaller black markings on terga 2–3. Male (Fig. 14): meso- and metanotum completely black. Mesepisternum usually completely black, rarely pale above. At least abdominal tergum 1 largely black, often with some black markings medially on following terga, but one or more middle terga always completely pale. Penis valve: ventral spine slightly longer than dorsal one; dorsal spine basally wide relative to length (Figs 30–31). The penis valve is thus more similar to that of *parcivalvis* (Figs 34–35) than *testaceipes* (Figs 32–33).

Total number of specimens examined: 35.

Similar species. Only very pale specimens of *testaceipes* (Fig. 15), found in warmer parts of central and southern Europe, but not in Fennoscandia, are likely to be confused with *stilata* (Fig. 12). However, the palest female *testaceipes* specimens have parts of the mesoscutum pale-marked, whereas the mesoscutum of *stilata* is always

completely black. Perhaps the shape of the tangium may be diagnostic, but this needs to be checked for a larger number of specimens: in *stilata* tangium roughly triangular and higher in proportion to length (Fig. 25) than the proportionately lower and more rhomboid tangium of *testaceipes* (Fig. 26).

Life history. Host plants: only *Crataegus* species have been reliably recorded as larval hosts. Brischke (1883: 168) mentions *C. laevigata* (=*oxyacantha* auct.). Cameron (1875) mentioned larvae identified as *stilata* from *Sorbus torminalis*, but the record might refer to *testaceipes*.



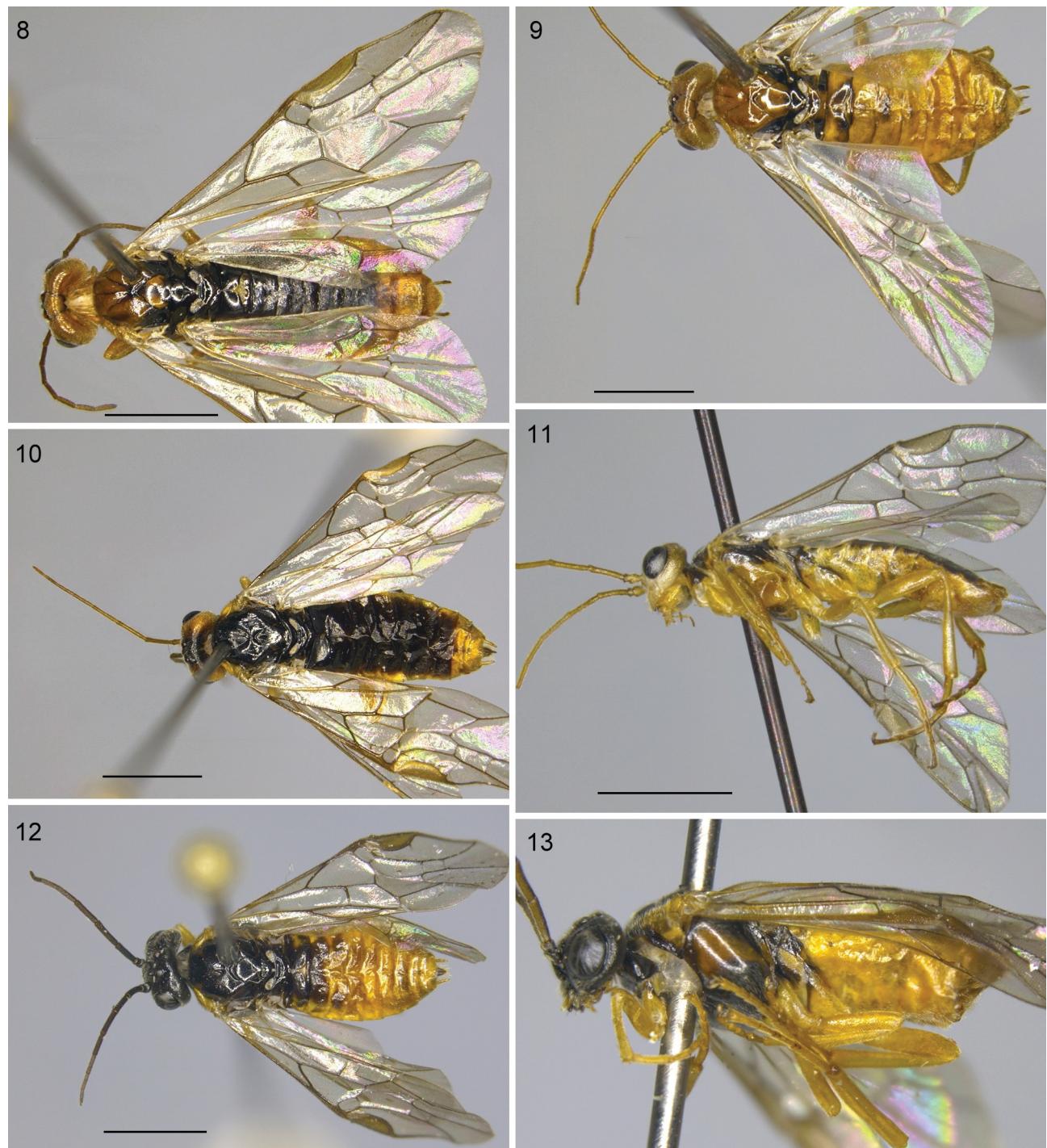
FIGURES 2–7. *Dineura* species. 2 *testaceipes* larva on *Sorbus intermedia* (80496). 3 *virididorsata* ♀, head, dorsal (31795). 4 *virididorsata* ♀, head, frontal (15244). 5 *virididorsata* ♂, head, dorsal (19664; formerly det. *pullior*). 6 *virididorsata* ♀, head, frontal (31792; formerly det. *pullior*). 7 *stilata*, head, frontal (31797).

Distribution. Widely distributed through most of Europe, including the British Isles, but not recorded in the Iberian Peninsula (Taeger *et al.* 2006). Not definitely known from outside Europe: according to Zhelochovtsev &

Zinovjev (1995), mentions of *stilata* from Siberia may refer to *parcivalvis*. However, *stilata* identified by Verzhutskii (1981) in Siberia is apparently *testaceipes* (see below). Occurrence in Sweden: published records; southern Sweden (Thomson 1871, as *Nematus stilatus*: the description clearly characterises the adults of *stilata*, but the host is wrongly given as “Rönn” [rowan, *Sorbus aucuparia*]), Skåne (Kullaberg) (Andersson 1962, Benander 1966). Material examined: Öland.

Specimens examined. Austria: 1♀ (DEI-GISHym31797), Upper Austria, Annaberg, reared from *Crataegus*, 01–30.09.1987, leg. E. Altenhofer (SDEI). 1♀ (BC ZSM HYM04507), Lower Austria, Zwettl, 25.08.1998, leg. M. Kraus (ZSM).

Germany: 12♀, 13♂, SDEI, ZMHUB, ZSM, including: Mecklenburg-Vorpommern, 1♀ (DEI-GISHym11350), Dambeck, 20.05.2011, leg. H.-J. Jacobs (SDEI)



FIGURES 8–13. *Dineura* species. **8** *virididorsata* ♀, dorsal (31794). **9** *virididorsata* ♀, dorsal (31798). **10** *virididorsata* ♀, dorsal (19239; formerly det. *pullior*). **11** *virididorsata* ♂, lateral (19664; formerly det. *pullior*). **12–13** *stilata* ♀, dorsal, lateral (31797). Scale bars 2 mm.

Sweden: Öland: 1♂ (NHRS-HEVA000003428) [no further data], leg. Boheman (NHRS). 2♂ (DEI-GIS-Hym31796), Station Linné 1km E, 40 m, 56.62°N 16.51°E, 29.05.2013, Liston, Prous & Taeger (SDEI). 1♂, same data as previous, but 30.05.2013. 1♂, same data as previous, but leg. Liston, 17.06.2016. 1♂, Mörbylånga kommun, Gamla Skogsby (Kalkstad), “diversitetsängen”, 56.62°N 16.51°E, 20.05.–28.06.2006, leg. SMTP (NHRS). 1♂, same data as previous, but 01–16.06.2005.

Dineura testaceipes (Klug, 1816)

Tenthredo (Allantus) testaceipes Klug, 1816: 84. Holotype ♀ (GBIF-GISHym2761, images: <https://doi.org/10.6084/m9.figshare.7851425>), die Gegend um Wien [Austria, environs of Vienna], in ZMHUB, examined.

Dineura ventralis Zaddach, 1859: 10. Syntypes ♀♂, bei Danzig [Poland, near Gdansk], material lost. Mentioned as synonym of *testaceipes* by Dalla Torre (1894).

Pontania ancilla Konow, 1901a: 82, 89–90. Syntypes ♀, Germania (in montibus Erzgebirge); lectotype ♀ designated by Muche (1970), in SDEI (GBIF-GISHym4138, images: <https://doi.org/10.6084/m9.figshare.7851440>). Type locality: Germany, Ore Mts.

Dineura testaceipes var. *nigriventris* Enslin, 1915: 321. Syntypes, sex not stated, type locality not stated; lectotype ♀ here designated, in ZSM (GBIF-GISHym3090, images: <https://doi.org/10.6084/m9.figshare.7851443>). Type locality: Germany, Lower Saxony, Liebenburg.

Additional description. Body length: ♀ 5.0–6.5mm, ♂ 4.2–5.5. Pterostigma uniformly pale, or darkened on margins, or near unicolorous brown; sometimes with base paler than rest. Female (Figs 15–16): Head black, except for pale labrum, sometimes whole clypeus, and more or less supraclypeal area; antenna from completely black to completely pale. Thorax black: darkest specimens with only tegula and upper posterior corner of pronotum pale; palest specimens with tegula, whole pronotum, broad margins of mesoscutal lobes, anterior of mesoscutellum, and mesepisternum except for ventral quarter pale. Abdomen from nearly completely black, except for pale hypopygium, valvifer 2, and cerci, to extensively pale on all sterna and downturned lateral parts of terga, with terga 8–10 completely pale; dorsum of terga 1–7 always mainly black. Lancet: Fig. 26. Male: range of variability similar to female. Penis valve: ventral spine much longer than dorsal one; ventral spine gradually tapering after medial constriction, and distal portion much longer than basal portion (Figs 32–33).

Total number of specimens examined: 35.

Similar species. *Dineura testaceipes* is very similar in coloration to *parcivalvis*, including the range of variability. Females of these species can be distinguished by the proportions of the apical flagellomeres (Figs 19–20), whereas the difference between males is perhaps too slight to be of practical use (Figs 21–22). Possibly the shape of the tangium may be diagnostic, but this needs to be checked for a larger number of specimens: in *parcivalvis* tangium roughly triangular and higher in proportion to length (Fig. 27) than the proportionately lower and more rhomboid tangium of *testaceipes* (Fig. 26). Males can be distinguished by their penis valves (see key). Only very pale specimens of *testaceipes*, found in warmer parts of central and southern Europe but not Fennoscandia, are likely to be confused with *stilata*: see under that species.

Life history. Host plants: *Sorbus aucuparia* is the main host, recorded independently by many authors (e.g. Kangas 1985, Macek 2015), but in Europe also fed upon are *Sorbus aria* (Liston *et al.* 2012; reared by E. Altenhofer, unpublished), *S. intermedia* (Fig. 2: see below, under Uppland, Arlanda Airport), *Crataegus* spp. (Macek 2015), and *Cotoneaster* sp. (Benander 1966; and recorded in Siberia from *C. melanocarpa* [sic! recte *melanocarpus* G. Lodd.] by Vershutskii (1981), as *stilata*). Verzhutskii (1981) described rearing larvae with conspicuous, apically bifid setae found in East Siberia on *Crataegus* sp. and *Cotoneaster melanocarpus*. According to current knowledge (see particularly Macek 2015), these do not belong to *stilata* (larvae with shorter, non-bifid setae) or *parcivalvis* (larva unknown, but only host supposed to be *Prunus padus*), but were probably *testaceipes*. Perhaps the record published by Cameron (1875) of larvae identified as *stilata* on *Sorbus torminalis* also refers to *testaceipes*.

Distribution. Northern and central Europe, including Britain and Ireland (Taeger *et al.* 2006), and Transpalaearctic to the southern Russian Far East (Zhelochovtsev & Zinovjev 1995). Occurrence in Sweden: published records; Skåne (Lindholmen and Ringsjön) (Thomson 1871, as *Nematus testaceipes*), Skåne (Kullaberg) (Benander 1966). Material examined: Skåne, Öland, Östergötland, Västmanland, Dalarna, Lycksele Lappmark.

Specimens examined. Austria: 1♂ (DEI-GISHym31800), Zwettl, Annatsberg, 1–30.09.1988, reared *Sorbus aucuparia*, leg. E. Altenhofer (SDEI). 1♀, 1♂ (DEI-GISHym19240, 19241), Lower Austria, Kirchberg am Walde,

reared *Sorbus aucuparia*, em. 29.05.2004, leg. E. Altenhofer (SDEI). 1♂, Lower Austria, Araburg, coll. 3.10.1987 as larva *Sorbus aria*, leg. E. Altenhofer (SDEI).

Estonia: 1♂ (DEI-GISHym31233), Jõgevamaa, Mustvee 1.8 km S, 40 m., 58.83°N 26.94°E, 04.06.2015, leg. Liston, Prous & Taeger (SDEI). 1♀, Lääne-nemaa, Karuse 1 km S, 25 m, 58.61°N 23.70°E, 06.06.2015 (SDEI).

Finland: 3♀ (SDEI), including 1♀ (DEI-GISHym19623), Hämeenlinna, Mootrata, suolenkki, 30.05.2009, leg. I. Kakko (SDEI).

Germany: 6♀, 3♂ (SDEI, ZSM).

Scotland: 1♀ (SDEI).

Sweden: Skane: 1♀, Ellestadssjön, 16.06.1969, leg. H. Andersson (MZLU). Öland: 1♀ (NHRS-HEVA000003429), Färjestaden, 56.65°N 16.45°E, 1.7.1928, leg. Wieslander (NHRS). 1♀, Station Linné 1km E, 40 m, 56.62°N 16.51°E, 29.05.2013, Liston, Prous & Taeger (SDEI). 1♀, Byxelkrok 2km SE, 17.06.2016, leg. Liston (SDEI). Östergötland: 2♀ 4♂ (NHRS-HEVA000005867 to 5872) [no further data], leg. Haglund (NHRS). Uppland: 1 larva (DEI-GISHym80496), Arlanda Airport, near Terminal 5, *Sorbus intermedia*, 08.08.2017, leg. Liston & Prous (SDEI). Västmanland: 1♀ (DEI-GISHym20597), Lindesberg 11km NW, 90 m, 59.67°N 15.14°E, 01.06.2013, Liston, Prous & Taeger (SDEI). Dalarna: 1♂ (NHRS-HEVA000005873), Särna, 61.68°N 13.13°E, 07.1907 (NHRS). Lycksele Lappmark: 1♂ (NHRS-HEVA000005875), Sorsele, 65.53°N 17.50°E, 14.07.1928, leg. Gaunitz (NHRS). Lapponia borealis: 1♀ (NHRS-HEVA000005874) (NHRS).

***Dineura virididorsata* (Retzius, 1783)**

Tenthredo viridi-dorsata Retzius, 1783: 73, by indication on Degeer (1771: p. 1002–1004 & plate 38 figs 8–10). Syntypes, larvae and adults (sex not stated), type locality presumably near Degeer's residence in Lövstabruk (Sweden, Uppland Province). Type material lost.

Tenthredo nigricans Christ, 1791: 446–447, by indication on Degeer (1771: p. 1002–1004 & plate 38 figs 8–10). Syntypes, larvae and adults (sex not stated), type locality presumably near Degeer's residence in Lövstabruk (Sweden, Uppland Province). Type material lost.

Tenthredo (Allantus) geeri Klug, 1817: 213–214, by indication on Degeer (1771: p. 1002–1004 & plate 38 figs 8–10). Syntypes, larvae and adults (sex not stated), type locality presumably near Degeer's residence in Lövstabruk (Sweden, Uppland Province). Type material lost.

Nematus degeeri: Thomson (1871), misspelling of *geeri* Klug.

Nematus varius Serville, 1823: 71–72. Syntypes ♂, Paris, types lost (Lacourt 2000). Types are the same specimens as for *N. varius* Lepeletier.

Nematus varius Lepeletier, 1823: 69. Syntypes ♂, Paris, types lost (Lacourt 2000). Listed as synonym of *virididorsata* by Dalla Torre (1894). Types are the same specimens as for *N. varius* Serville.

Nematus hartigii Gimmerthal, 1844: 37–38. Holotype ♀, in der Nähe von Riga [Latvia, near Riga], specimen probably lost. Listed as synonym of *virididorsata* by Dalla Torre (1894).

Dineura virididorsata var. *dorsalis* Enslin, 1915: 319. Syntypes ♀♂, type locality not stated; **lectotype** ♀ here designated, in ZSM (GBIF-GISHym3089, images: <https://doi.org/10.6084/m9.figshare.7851458>). Type locality: Finland, Karisjo. Paralectotype: 1♂ (GBIF-GISHym3088), in ZSM.

Dineura pullior Schmidt & Walter, 1995: 387–392. Holotype ♀ (GBIF-GISHym3697, images: <https://doi.org/10.6084/m9.figshare.7856741>), in ZSM. Type locality: Finland, Kevo, Utsjoki. **New synonym**.

Taxonomy. According to Schmidt & Walter (1995), *Dineura pullior* occurs in Europe only north of 68°N, together with *virididorsata*, although *pullior* is by far the more common. We found that none of the morphological characters which was stated by Schmidt & Walter (1995) to distinguish *pullior* from *virididorsata* is stable. Although there is clearly a tendency towards a darker colour pattern and smaller body size in high northern areas (the form named *pullior*), the differences described in the lancets of the two nominal species (Figs 23–24) are not completely correlated with colour pattern, and individuals with intermediate types of lancet setation and tangium shape were found (additional images: <https://doi.org/10.6084/m9.figshare.7873466>). Perhaps the extreme variability in the size and number of setae is correlated with body size: smaller females having fewer setae. The shape of the tangium is also apparently variable, but can be difficult to interpret because of distortion during preparation. Schmidt & Walter (1995) stated “In the male of *D. pullior* the dorsal edge of the valvispina, viewed laterally, tapers evenly to an acute apex (Fig. 9), whereas that of *D. virididorsata* is sharply angled (Fig. 10)”. The difference, even as illustrated in their paper, is extremely slight. We detected no significant differences in penis valves of specimens tentatively determined ac-

cording to colour pattern and provenance (Figs 28–29). Nor do COI or nuclear sequences distinguish these forms, although nuclear genes were sequenced only for a single male attributed to *pullior* (barcode of which is identical to a female from the type locality). Having been unable to find any reliable morphological or genetic characters which will separate them, we here propose the synonymy of *pullior* with *virididorsata*.



FIGURES 14–22. *Dineura* species. **14** *stilata* ♂, dorsal (31796). **15** *testaceipes* ♀, dorsal (19240). **16** *testaceipes* ♀, dorsal (19623). **17** *parcivalvis* ♀, lateral (11575). **18** *parcivalvis* ♂ [“Allotype”], lateral (<http://id.luomus.fi/GL.2412>). Scale bars 2 mm. **19** *testaceipes* ♀, apical antennomeres (20597). **20** *parcivalvis* ♀, apical antennomeres (11575). **21** *testaceipes* ♂, apical antennomeres (31233). **22** *parcivalvis* ♂, apical antennomeres [“allotyp” FMNH].

Additional description. Body length: ♀ 4.9–8.0 mm, ♂ 4.9–7.0. Head from completely pale except for directly around ocelli and along upper postoccipital grooves (Figs 3–4), to extensively dark, with contiguous black marking covering postocellar and ocellar areas, reaching forward to toruli (Figs 5–6), and occiput mostly dark (Fig. 10).

Mesonotum from completely pale (Fig. 9) to completely dark (Fig. 10). Underside of thorax often entirely pale, but more or less black can be anepimeron, upper edge of mesepisternum, and mesepisternum ventrally. Abdomen from completely pale except for tergum 1 medially and narrow anterior edge of tergum 2 (Fig. 9), to extensively black on terga except for downturned lateral margins and more or less terga 8, 9, and 10 (Fig. 10). Antenna and legs entirely pale (except for more or less obscurely darkened tarsi and apices of tibiae). Female (Figs 8–10): lancet (Figs 23–24). Male (Fig. 11): penis valve (Figs 28–29).

Total number of specimens examined: about 270.

Similar species. *Dineura virididorsata* is easily distinguished from the other West Palaearctic species by its extensively pale orbits. *Dineura betulivora* Togashi, 1995 (Japan) is according to the original description very similar to the dark specimens of *virididorsata* formerly called *pullior*, and possibly not distinct, but we have not examined type specimens.

Life history. Host plants: *Betula pendula* and *B. pubescens* (including the varieties or subspecies *carpatica* and *czerepanovii*) (Pschorr-Walcher & Altenhofer 2000, Macek 2015), and rarely on *B. nana* (personal communication from V. Vikberg). A number of studies (several of which are cited by Schmidt & Walter 1995) deal with various aspects of the ecology and biology of *virididorsata* species in northern Fennoscandia. Some defoliation events have been recorded at high latitudes on mountain birch, e.g. by Koponen (1981) in northernmost Norway.

Distribution. Through most of northern and central Europe, including Britain and Ireland (Taeger *et al.* 2006), south to the Iberian Peninsula (Liston 2016), and Transpalaearctic (Zhelochovtsev & Zinovjev 1995) through Russia (Zhelochovtsev & Zinovjev 1995) to Hokkaido, Japan (Togashi 1990) and Hubei Province, China (Wei & Nie 1998). Occurrence in Sweden: published records; distributed throughout the whole of Scandinavia (Thomson 1871, as *Nematus degeeri*). Material examined: Skåne, Halland, Småland, Öland, Gotland, Östergötland, Västergötland, Bohuslän, Södermanland, Uppland, Västmanland, Dalarna, Gästrikland, Härjedalen, Jämtland, Ångermanland, Häl-singland, Norrbotten, Lycksele Lappmark, Lule Lappmark, Torne Lappmark.

Specimens examined. Estonia: 1♀ (DEI-GISHym31798), Jõgevamaa, Mustvee 1.8km S, 40m, 04.06.2015, leg. Liston, Prous & Taeger (SDEI).

Finland: 11♀, 6♂ (SDEI, ZSM). Specimens formerly determined as *pullior*: 1♂ (DEI-GISHym11573), Nuor-gam 17km SSE, 69.94°N 28.04°E, 20.06.2001, leg. A. Taeger & C. Kutzscher (SDEI). 1♀ (DEI-GISHym19239), Kevo, 69.74°N 26.99°E, Malaise trap, 15–20.06.2001, leg. Taeger, Kraus & Kutzscher (SDEI). 1♂ (DEI-GIS-Hym19619), Kilpisjärvi, Fjelde Pikkumalla, 69.05°N 20.80°E, 24.06.2004, leg. M. Viiitasaari (SDEI). 1♀ (DEI-GISHym31792), Utsjoki, Isieskujoki 774:50, 09.06.1992, leg. M. Viiitasaari (SDEI). 1♀, 1♂ (DEI-GISHym31801, 31802), Utsjoki, 69.88°N 27.00°E, 1990, reared (SDEI).

Germany: 17♀, 3♂ (SDEI, ZSM).

Portugal: 2♀, see Liston (2016) (SDEI).

Russia: Kemerovo Region 2♀, 5♂ (Institute of Systematics and Ecology of Animals, Siberian Branch RAS, Novosibirsk). 2♀ (DEI-GISHym31810 and 31811; formerly determined as *pullior*), Primorskiy Kray, Sichote Alin, meteorological station 28km SE Chuguevka, 43.59°N 134.08°E, 01.06.1993, leg. A. Taeger (SDEI).

Scotland: 1♀ (SDEI).

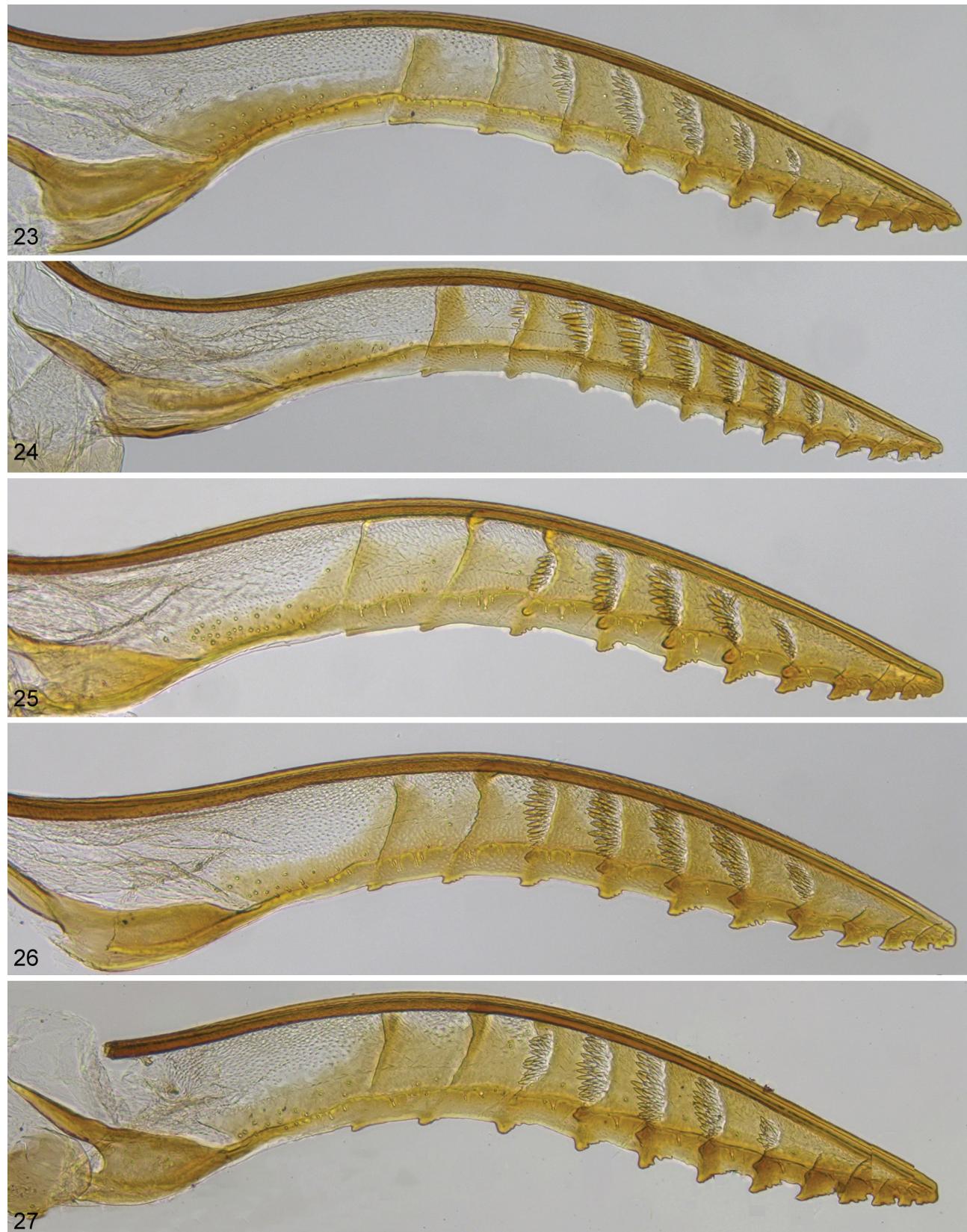
Sweden: 132♀, 48♂ (MZLU, NHRS, SDEI), including the following [other provinces: see under species treatment]. Torne Lappmark: 1♀ (DEI-GISHym15244), Abisko, Mt. Njulla, 400–700m, 29.06.2012, leg. Liston & Taeger (SDEI). 2♀ (DEI-GISHym31794, 31795), Abisko National Park, E10, 390m, 30.06.2012, leg. Liston & Taeger (SDEI). 1♀ (DEI-GISHym31809), Abisko, Mt. Njulla, 600–900m, 23.06.2016, leg. Liston (SDEI). 1♂ (DEI-GISHym80155), Abisko 6km W, 650–900m, 02.07.2016, leg. Liston & Prous (SDEI). 1♂ (DEI-GISHym19664; previously determined as *pullior*), Stordalen, 68.35°N 19.04°E, 17.06.2012, leg. A. Liston, A. Taeger & S. M. Blank (SDEI).

Unclarified species names in *Dineura*

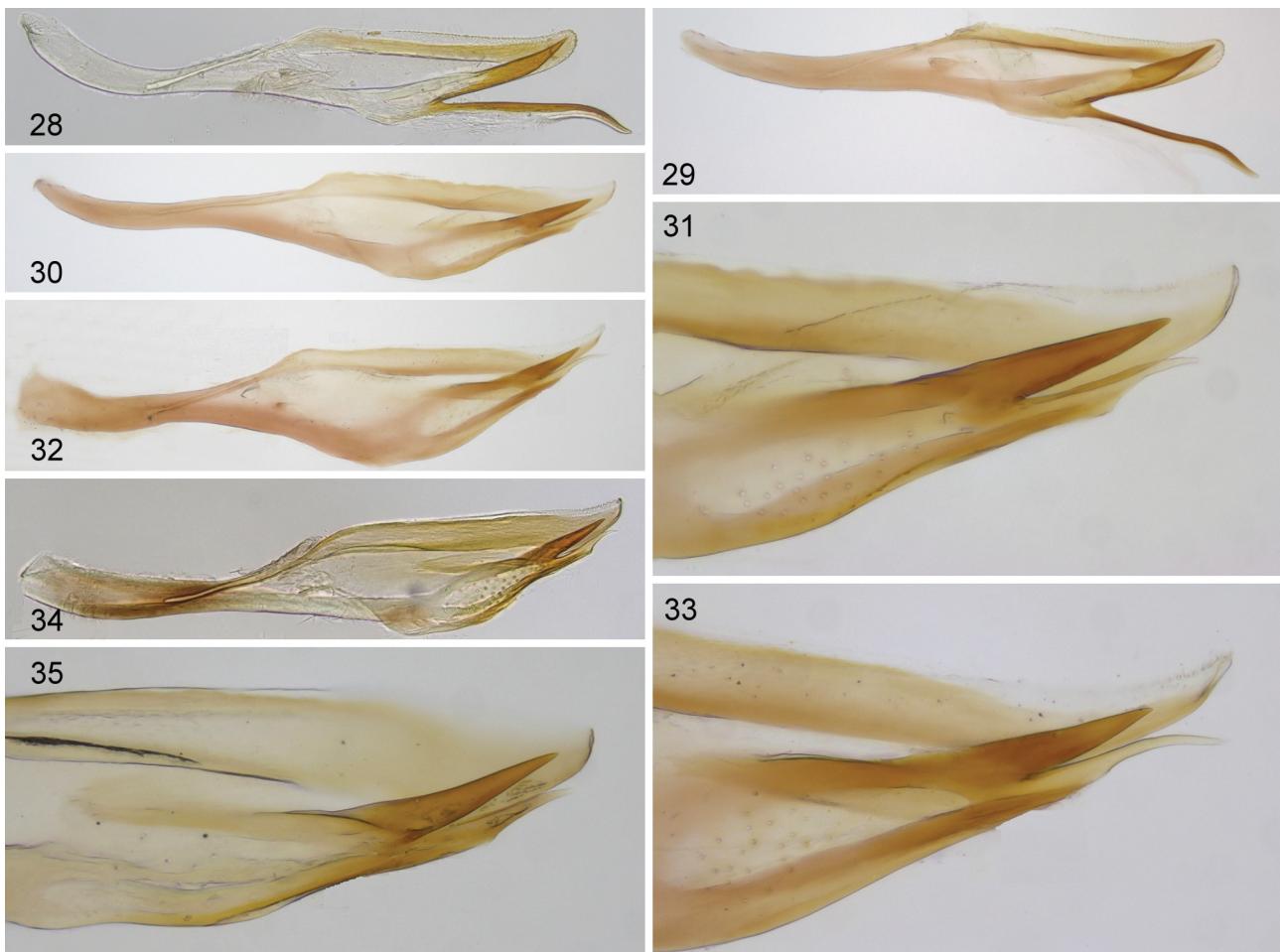
Dineura simulans Cameron, 1877: 155–156. Syntype(s) ♀, England, possibly in BMNH, not examined.

This taxon was treated as a synonym of *Pseudodineura fuscula* (Klug, 1816) by Konow (1905), followed by Taeger *et al.* (2010), but Enslin (1914) was sure that it must belong to the former genus *Pontania* (now synonymised with

Euura). Neither of these authors had seen the type of *D. simulans*. The original description contains insufficient information to place the taxon. However, “antennae filiform, nearly as long as the body” does not fit a known female *Pseudodineura* species, which have antennae only about as long as the abdomen. Until type material should be located, the name is better treated as a Nematinae species *incertae sedis*.



FIGURES 23–27. *Dineura*, lancets. **23** *virididorsata* ♀, lancet (31809). **24** *virididorsata* ♀, lancet (31801; formerly det. *pullior*). **25** *stilata* ♀, lancet (31797). **26** *testaceipes* ♀, lancet (19240). **27** *parcivalvis* ♀, lancet (11575).



FIGURES 28–35. *Dineura*, penis valves. **28** *virididorsata* ♂, penis valve (80155). **29** *virididorsata* ♂, penis valve (19664; formerly det. *pullior*). **30–31** *stilata* ♂, penis valve (11350). **32–33** *Dineura testaceipes* ♂, penis valve (31800). **34** *Dineura parcivalvis* ♂, Russian Far East, penis valve (80232). **35** *Dineura parcivalvis* ♂, Finland, penis valve [“allotyp” FMNH].

Discussion

After evaluating the currently available morphological, genetic and biological data, the taxonomy of *Dineura* occurring in Europe seems somewhat clearer than previously. In particular, the status of *stilata* and *testaceipes* as separate species, as recently upheld by Macek (2015), has received (weak) corroboration by the detection of small differences in the male genitalia. On the other hand, because we were unable to find any reliable way of distinguishing *virididorsata* and *pullior*, we have proposed their treatment as synonyms. Further study of some nuclear gene sequences suggests itself as the next step in trying to understand the genus better.

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